carolinensis (Mill.) Tidestrom), $2n = 16$, occurs in swampy or sandy soils in low, acid prairies, thickets and woods, principally along the Coastal Plain from southern New Jersey to southern Florida, west to eastern Texas and southeastern Oklahoma, and north to Arkansas. It also occurs in Bermuda, the Greater Antilles, Mexico, and Central America. Taxonomically important characters are the heavily resinous-glandular glabrescent branchlets; narrowly oblanceolate, coriaceous, persistent leaves, abundantly resinous-glandular on the upper surface; and glabrous fruit. The fruit is eaten by numerous coastal birds, including quail and apparently wild turkey in some areas.

Although *Myrica pusilla* Raf. (*Cerothamnus pumilus* (Michx.) Small), $2n = 16$, was recognized as a distinct species by both Fernald (Gray's Man. Bot. ed. 8, 1950) and Gleason (New Britton & Brown Illus. Fl. Northeast. U.S. Vol. 2. 1963), Radford, Ahles, & Bell (Man. Vasc. Fl. Carolinas, 1967) treated it as *M. cerifera* var. *pumila* Michx. It appears that *M. pusilla* is merely a smaller xeric form of *M. cerifera* that does not merit specific status (Thieret, 1966). Varietas *pumila* occurs on dry, sandy pinelands and prairies from eastern Texas and Louisiana, east to Florida and north to North Carolina. The status of this questionable variety should be investigated more thoroughly.

Section FAYA, characterized by simple or branched aments, carpellate spikelets with several flowers, of which only some develop, and fruits 4–6 mm. in diameter, includes only three species. *Myrica inodora* Bartr. occurs in our range; *M. californica* Cham. occurs only along the west coast of the United States from Washington south to California; and *M. Faya* Ait. is restricted to Madeira, the Canary Islands, the Açores, and Portugal (where it is naturalized or possibly indigenous). This type of distribution of closely related species is further evidence of the relict nature of the genus.

Lacking the almost characteristic myricaceous scent, *Myrica inodora* Bartr. (*Morella inodora* (Bartr.) Small; *Cerothamnus inodorus* (Bartr.) Small), odorless bayberry, occurs sparingly in the Gulf Coast pineland swamps from southeastern Louisiana to northwestern Florida. This evergreen shrub is recognized by its smooth, reddish-brown branchlets that are scurfy tomentose when young but later pubescent to glabrous; by its oblong-obovate to ovate coriaceous more or less glandular leaves with the margin usually entire, rarely with a few serrations apically; and by its glabrous fruit.

Subgenus MYRICA (subg. *Gale* [Duham.] Engler; *Gale* Duham.; *Cerophora* subg. *Galestis* Raf.; *Angeia* Tidestrom) includes *M. Gale* L. (*Gale palustris* (Lam.) Chev.), $2n = 48$, ca. 96, sweet gale, of northwestern Europe, northern North America, and northeastern Asia, and *M. Hartwegii* S. Wats., of the Sierra Nevada in California. Found principally in swampy areas, *M. Gale* is distributed in North America from Labrador to Alaska, south to Newfoundland, Long Island and Pennsylvania, west to Michigan, Minnesota, Wisconsin, and Washington and Oregon. It reaches our range in Tennessee and in bogs, now largely drained, in Henderson
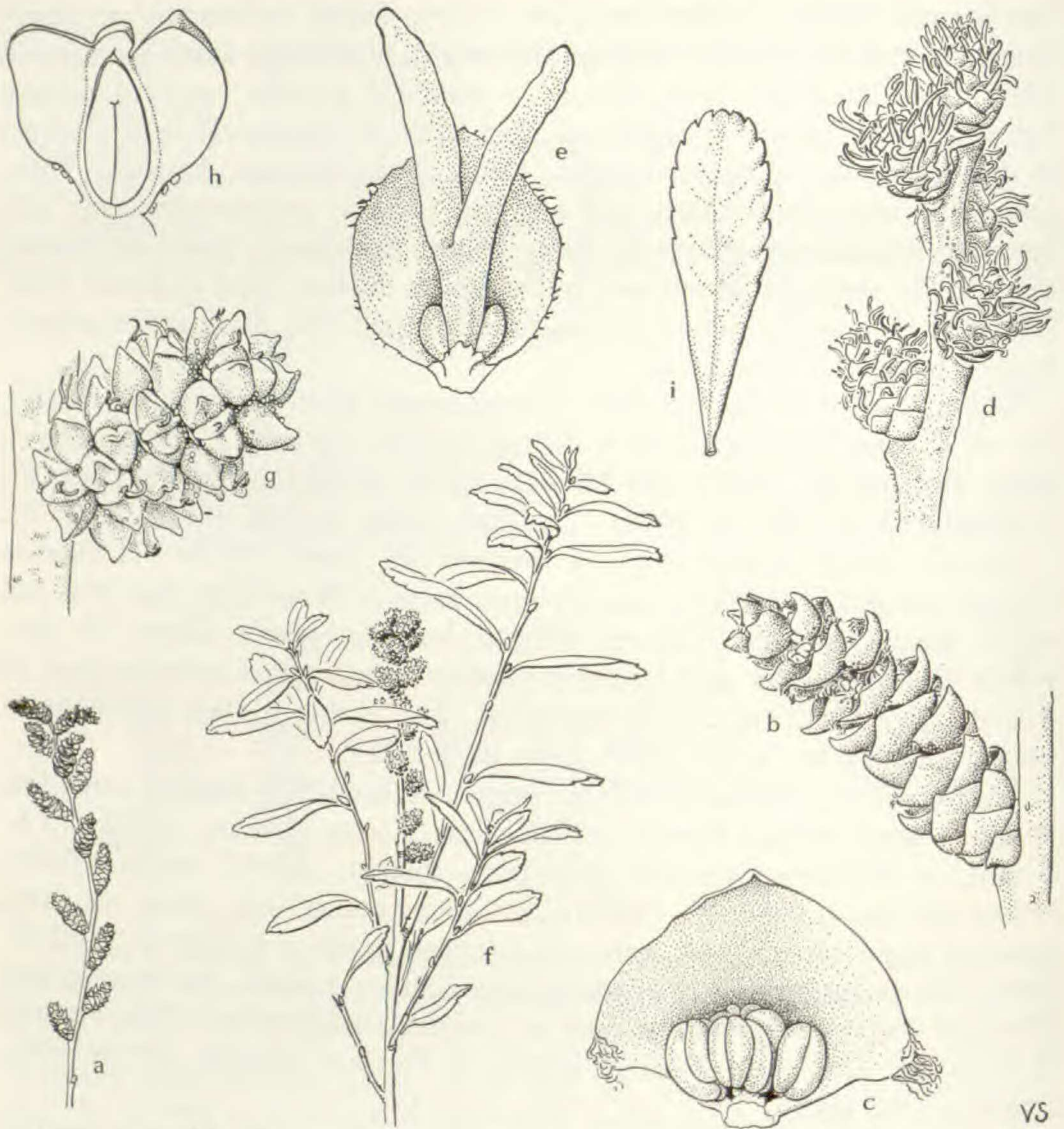
FIGURE 2. **Myrica** subg. **Myrica**. *M. Gale*: a, branchlet with staminate inflorescences, × 1/2; b, staminate inflorescence, × 3; c, staminate flower with bract, × 10; d, branchlet with carpellate inflorescences, × 4; e, carpellate flower with bract and two lateral secondary bracts, × 25; f, habit with mature fruits, × 1/2; g, mature fruits of a single carpellate inflorescence, × 4; h, semidiagrammatic longitudinal section of fruit, showing fleshy secondary bracts and embryo, × 12.

County, North Carolina. The species, as well as the subgenus, is characterized by aments borne near the summit of the branchlets of the preceding year; by the bract of the staminate flower longer than the stamens; by the smooth fruit each flanked by two accrescent, more or less fleshy secondary bracts; and by the lack of a heavy wax deposit on the surface of the fruits. The considerable variation in the amount of pubescence has led to the recognition of var. *subglabra* (Chev.) Fern. in eastern and var. *tomentosa* C. DC. in Pacific North America and Eurasia.

The few chromosome counts suggest that European populations of *M. Gale* are hexaploids ($2n = 48$), while those from western North America

are apparently dodecaploids ($2n$ = ca. 96 in plants from the Queen Charlotte Islands). Further counts are needed throughout the range of the species to determine the extent and levels of polyploidy and its significance.

An interesting phenomenon in *M. Gale* is the great plasticity in the sexes of individual flowers as well as individual plants. Three types of monoecious plants occur (Davy & Gibson, 1917): both staminate and separate carpellate aments may occur on the branchlets of a single plant; the branchlets may produce androgynous aments with staminate flowers on the lower part of the ament; or in some aments perfect proterogynous flowers capable of producing fruit can be found. In addition, the sex of a plant of *M. Gale* may vary from one year to the next, from undetermined causes.

Most, if not all, species of *Myrica* have numerous nodules on the roots, including the adventitious ones arising from prostrate stems or rhizomes. Recent investigations by Bond have clearly demonstrated that the nodules, especially those of *M. Gale*, are accumulators of nitrogen. Bond (1958) postulated that the nitrogen fixing nodules of *Myrica* species may have been the original and principal source of symbiotic nitrogen in temperate regions following the Pleistocene.

Known best to the nonbotanist for their role in candle making, *Myrica cerifera*, *M. pensylvanica*, *M. heterophylla*, and to a lesser extent, *M. inodora* were sought by early settlers of the eastern United States. The fruits were gathered in the fall and placed in boiling water, the waxlike coating (a fat composed mainly of palmitin or palmitic acid) then melting and rising to the surface was skimmed off for use in candle making. Today most bayberry candle fat is imported into the United States from South America. In the eastern United States the making of bayberry candles with locally gathered fat has become a novelty or tourist attraction. In Europe bayberry fat is used in the manufacture of soap, probably for its pleasant scent.

Of limited economic importance, the buds and mainly the fruits serve as a food source for wildlife, especially birds. Muskrats have been observed feeding upon the fruits of *M. Gale*, and the buds and aments are eaten by sharp-tailed deer. The bark of *Myrica cerifera* and *M. pensylvanica* were once used in moderate amounts as an astringent and in larger amounts as an emetic. The bark in the form of a powder or in a decoction was also used to treat inflammations, ulcers, and many other internal problems. It has been reported that the leaves can be used as a substitute for bay leaves (*Laurus nobilis* L.) in flavoring stews and soups. Because of their habit of growth various species are effective in controlling erosion. Several species are attractive ornamental shrubs in cultivation.

REFERENCES:

Under family references see E. C. ABBE; L. B. ABBE; HJELMQVIST; RENDLE; SARGENT, pp. 163–167; VINES, pp. 117–120; and YOUNGKEN.

BARTON, L. V. Germination of bayberry seeds. Contr. Boyce Thompson Inst. 4: 19–25. 1932.

BOND, G. Root nodules of bog myrtle or sweet gale (*Myrica Gale* L.). Nature 163: 730. 1949.

———. The fixation of nitrogen associated with the root nodules of *Myrica Gale* L., with special reference to its pH relation and ecological significance. Ann. Bot. II. 15: 447–459. *pl. 19.* 1951.

———. Some features of root growth in nodulated plants of *Myrica Gale* L. *Ibid.* 16: 467–475. *pls. 23, 24.* 1952.

———. Nitrogen fixation in some non-legume root nodules. Phyton Buenos Aires 24: 57–66. 1967. [Includes *M. Gale.*]

BOTTOMLEY, W. B. The root-nodules of *Myrica Gale*. Ann. Bot. 26: 111–117. *pls. 11, 12.* 1912.

BURTT, B. L. Leaf-colour forms in *Myrica Gale*. Jour. Bot. 77: 91–93. 1939.

DAVEY, A. J., & C. M. GIBSON. Note on the distribution of sexes in *Myrica Gale*. New Phytol. 16: 147–151. *pl. 1.* 1917.

DAVIDSON, R. W., W. A. CAMPBELL, & G. F. WEBER. *Ptychogaster cubensis*, a wood-decaying fungus of southern oaks and waxmyrtle. Mycologia 34: 142–153. 1942. [*M. cerifera.*]

DODGE, B. O., & J. F. ADAMS. Notes relating to the *Gymnosporangia* on *Myrica* and *Comptonia*. Mycologia 9: 23–29. *pls. 2, 3.* 1917.

FATALIEV, R. A. Representatives of the genera *Glyptostrobus*, *Quercus* and *Myrica* in the Upper Sarmatian flora of Mt. Katar in Transcaucasia. (In Russian.) Bot. Zhur. 47: 1817–1822. *pls. 1, 2.* 1962. [*M. lignitum*, *M. vindobonensis.*]

FERNALD, M. L. The glabrous-leaved sweet gale. Rhodora 16: 167. 1914.

———. Midsummer vascular plants of southeastern Virginia. *Ibid.* 37: 378–413, 423–454. *pls. 384–405.* 1935. (Reprinted as Contr. Gray Herb. 109.) [*M. Curtissii* Chev. var. *media* (Michx.) Chev., 423, 424.]

———. Noteworthy plants of southeastern Virginia. *Ibid.* 40: 364–424, 434–459, 467–485. *pls. 509, 535.* 1938. (Reprinted as Contr. Gray Herb. 123.) [*M. pusilla*, *M. heterophylla*, and *M. heterophylla* var. *Curtissii* (Chev.) Fern., comb. nov., 408–410.]

FLETCHER, W. W. The development and structure of the root-nodules of *Myrica Gale* L. with special reference to the nature of the endophyte. Ann. Bot. II. 19: 501–513. *pls. 18, 19.* 1955.

GLADKOVA, A. N. On the pollen of certain living and fossil species of the genus *Myrica* L. (In Russian.) Dokl. Akad. Nauk SSSR. 109: 213–216. 1956.*

GRAY, J. Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. Science 132: 808–810. 1960. [Includes *Myrica.*]

HÅKANSSON, A. Endosperm formation in *Myrica Gale* L. Bot. Not. 108: 6–16. 1955.

HARA, H. Contributions to the study of variations in the Japanese plants closely related to those of Europe or North America. Part. 1. Jour. Fac. Sci. Univ. Tokyo Bot. 6: 29–96. 1952. [*M. Gale*, *M. Gale* var. *tomentosa*, *M. Gale* var. *subglabra*, 32]

HULTÉN, E. The amphi-Atlantic plants and their phytogeographical connections. Sv. Vet.-Akad. Handl. IV. 7: 1–340. *map.* 1958. [*M. Gale*, 218, *map 199.*]

HYLANDER, N. Nomenklatorische und systematische Studien über nordische Gefässpflanzen. Uppsala Univ. Arsskr. 1945. 7: 1–338. 1945. [*M. cerifera* as lectotype species, 40.]

KERSHAW, E. M. The structure and development of the ovule of *Myrica Gale*. Ann. Bot. **23**: 353–362. *pl. 24*. 1909.

KREMBS, A. G., JR. The structure of the stems of *Myrica Gale* L. and *Myrica cerifera* L. Pharm. Arch. **4**: 128–136. *pls. 3, 4*. 1901.

LEAF, G., I. C. GARDNER, & G. BOND. Observations on the composition and metabolism of the nitrogen-fixing root nodules of *Myrica*. Biochem. Jour. **72**: 662–667. 1959.

MACKINTOSH, A. H., & G. BOND. Diversity in the nodular endophytes of *Alnus* and *Myrica*. Phyton Buenos Aires **27**: 79–90. 1970.

NIEUWLAND, J. A. The name of our American wax bayberries. Am. Midl. Nat. **1**: 238–243. 1910.

RAYCHAUDHURI, S. P. Studies on bayberry yellows. Phytopathology **43**: 15–20. 1953. [*M. carolinensis.*]

REED, C. F. *Myrica pensylvanica*, a new host for *Phoradendron flavescens* in Virginia. Castanea **25**: 86. 1960.

SARGENT, C. S. The wax-myrtles of the sea-coast of eastern North America. Garden Forest **7**: 474, 475. *figs. 75, 76*. 1894.

SCHOEMAN, D. J., & F. HAWKE. The fruitcoat fat of *Myrica cordifolia* — cape berry wax. I. Physical and chemical constants and fatty acid composition. Jour. S. Afr. Chem. Inst. II. **1**: 5–13. 1948.*

STEWART, W. D. P. Nitrogen-fixing plants. Science **158**: 1426–1432. 1967. [Includes *M. Gale.*]

TAYLOR, J. B., & J. N. JOINER. Rooting response of *Feijoa sellowiana* and *Myrica rubra* as affected by 2, 3, 5-triiodobenzoic acid and 3-indolebutyric acid. Proc. Florida State Hort. Soc. **73**: 363–366. 1960.*

TAYLOR, L. A. Plants used as curatives by certain southeastern tribes. xi + 88 pp. Botanical Museum, Harvard University. 1940. [*M. cerifera*, 13, 14.]

TAYLOR, R. L., & G. A. MULLIGAN. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. Canada Dep. Agr. Monogr. 4, Part 2. ix + 148 pp. 1968. [*M. Gale*, $2n =$ ca. 96, p. 52.]

THIERET, J. W. Habit variation in *Myrica pensylvanica* and *M. cerifera*. Castanea **31**: 183–185. 1966.

VIKHIREVA, V. V. Anatomical structure and development of the pistillate blossom of sweetgale, *Myrica Gale* L. (In Russian.) Acta Inst. Bot. Acad. Sci. URSS 7. Morphol. Anat. Pl. **4**: 270–287. 1957.*

YEN, T. K. Structure and development of the flower and the fruit of *Myrica rubra*. (In Chinese.) Peking Nat. Hist. Bull. **19**: 2–20. 1950.*

YOUNGKEN, H. W. Studies of the bark of *Myrica cerifera* Linn. Jour. Am. Pharm. Assoc. **12**: 484–488. 1923.*

2. Comptonia L'Heritier ex W. Aiton, Hort. Kew. 3 : 334. 1789.

Low-growing shrubs; branches terete, brown, villous to minutely puberulent, fragrant. Leaves appearing after flowering, pinnatifid with rounded lobes, membranaceous, linear-lanceolate, deciduous or persisting until the following spring, glabrous to densely pubescent, short-petiolate; stipules present, semicordate becoming subfoliaceous, deciduous. Plants monoecious or dioecious; flowers usually imperfect, borne in axillary aments. Staminate flowers in cylindrical, flexuous aments near the apex of the branchlets; primary bract cordate, reniform; stamens 3–8; filaments free. Carpellate flowers generally in erect globose-ovoid aments,
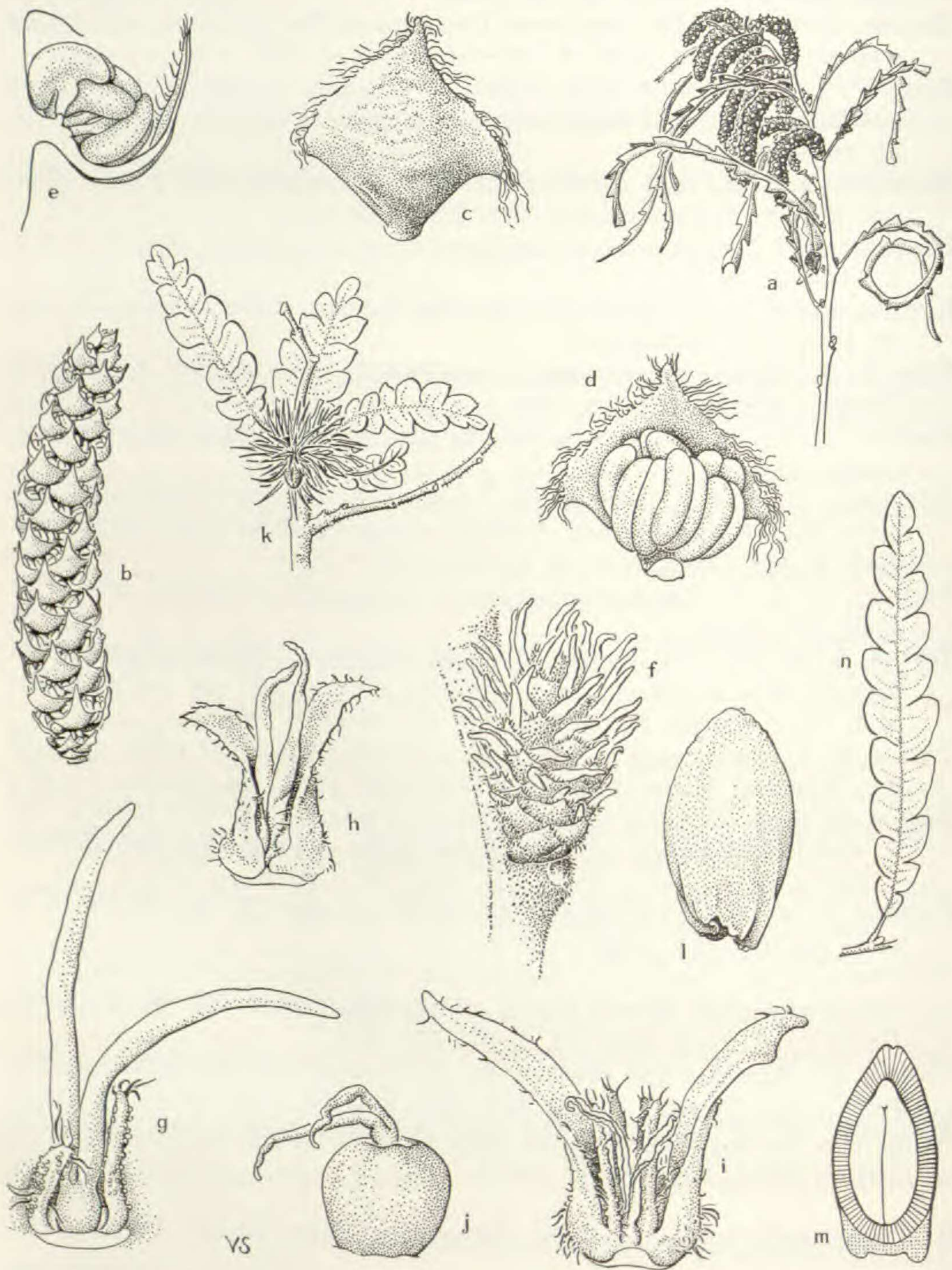
FIGURE 3. **Comptonia.** *C. peregrina*: a, branchlet with staminate inflorescences, × 1/2; b, staminate inflorescence, × 3; c, bract of staminate flower, × 12; d, staminate flower with bract, × 12; e, lateral view of staminate flower in partial section, × 12; f, carpellate inflorescence, × 6; g, carpellate flower at time of pollination, × 25; h, carpellate flower following fertilization showing development of primary bracts, × 12; i, carpellate flower after fertilization showing development of both primary and secondary bracts, × 12; j, young fruit with semipersistent styles, × 6; k, branchlet with mature fruit and accessory bracts, × 1; l, mature fruit, × 6; m, semidiagrammatic longitudinal section of mature fruit to show embryo, × 6; n, mature leaf, × 1.

usually on older wood, the primary bract usually ovate, pubescent, at least near the base; each flower subtended by 6–8 minute linear to acicular secondary bracts that persist and elongate in fruit (see FIGURE 3, g–i, k). Fruit a small ovoid-oblong, smooth, shining nut. TYPE SPECIES: *C. aspleniifolia* (L.) L'Her. ex W. Ait. = *C. peregrina* (L.) Coult. (Name commemorating H. Compton, 1632–1713, an amateur horticulturist and supporter of botany, who also served as Bishop of London.) — SWEET FERN.

A single extant species, *Comptonia peregrina* (L.) Coult., $2n = 32$, sweet fern, found on poor, often rather dry soils in woodlands, clearings, pastures, and pine barrens from Nova Scotia to Saskatchewan, south to Virginia, western North Carolina (but also in four counties in the lower Piedmont), extreme western South Carolina, and locally in northern Georgia and Tennessee, Ohio, northwestern Indiana, Illinois and Minnesota. The rather attractive low shrub with its fragrant aroma when crushed has been separated into two varieties. The questionably distinct var. *aspleniifolia* (L.) Fern., of the Coastal Plain pinelands or pine barrens from Long Island, New York, to Virginia, is characterized by the minutely puberulent branchlets, sparsely short-puberulent or glabrous leaves, and fruits 3–4 mm. long. The more northern and inland var. *peregrina* has more or less pilose branchlets, pilose leaves, and fruits 4–5 mm. long.

The six to eight secondary bracts associated with a single pistillate flower suggest that the solitary flower is derived by reduction from a few-flowered cyme. The inner secondary bracts would be the only grossly observable remnants of the cyme. A second possibility is that the inner secondary bracts are actually modified perianth parts that are completely lacking in *Myrica*. A careful anatomical study of the flowers and aments is needed.

Comptonia peregrina is the only survivor of a genus that had perhaps a dozen species in the Eocene and Oligocene. Berry (1906) postulated that *Comptonia* developed in the Upper Cretaceous as a branch from *Myrica* stock, but supporting evidence is lacking. Numerous Tertiary fossils of *Comptonia* clearly demonstrate that several species once occupied regions throughout much of the temperate world. In European Tertiary deposits, *C. difformis* (Sternh.) Berry is the most common fossil species of the genus (Kotlaba, 1967).

REFERENCES:

Under family references see E. C. ABBE; L. B. ABBE; HJELMQVIST, RENDLE, and YOUNGKEN.

BERRY, E. W. Living and fossil species of *Comptonia*. Am. Nat. **40**: 485–524. 1906.

DODGE, B. O., & J. F. ADAMS. Notes relating to the *Gymnosporangia* on *Myrica* and *Comptonia*. Mycologia **9**: 23–29. *pls. 2, 3.* 1917.

FERNALD, M. L. Noteworthy plants of southeastern Virginia. Rhodora **40**: 364–424, 434–459, 467–485. *pls. 509–535.* 1938. (Reprinted as Contr. Gray Herb. 123.) [*Comptonia*, 410–412, *pl. 514*, including *C. peregrina* var. *aspleniifolia* (L.) Fern., comb. nov.]

Fox, W. B., R. K. GODFREY, & H. L. BLOMQUIST. Notes on distribution of North Carolina plants — II. Rhodora **52**: 253–271. 1950. [*C. peregrina*, 261.]

HEINO, H. E. The excised embryo culture method for controlled seedling growth of the sweet fern, *Comptonia peregrina*, of the family Myricaceae. Proc. Minn. Acad. Sci. **29**: 180–184. *map.* 1961.

KOTLABA, F. Taxonomic-nomenclatural notes on the fossil *Comptonia difformis* (Sternb.) Berry and the recent *Comptonia aspleniifolia* (L.) Aiton. (In Czech; English summary.) Preslia **33**: 130–140. 1961.

RODRIGUEZ-BARRUECO, C. The occurrence of nitrogen-fixing root nodules on non-leguminous plants. Bot. Jour. Linn. Soc. London **62**: 77–84. *1 pl.* 1969. [Includes 12 spp. of *Myrica*.]

ZIEGLER, H. "Rhizothamnien" bei *Comptonia peregrina* (L.) Coult. Naturwissenschaften **47**: 113, 114. 1960. [See also Mitt. Deutsch. Dendrol. Ges. **61**: 28–31. 1960.]

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, VII.
ADDITIONAL NOTES ON ACROTREMA

William C. Dickison

I have pointed out during this series of papers that the Dilleniaceae is comprised of genera possessing considerable morphological diversity, a result in part of the wide range of growth habits encountered. One of the most interesting, yet least studied genera in the family, is *Acrotrema* Jack, a rhizomatous, semi-herbaceous plant.

Acrotrema is of interest not only because it is a small, nearly herbaceous plant in an otherwise woody family (the Australian genus *Pachynema* is also for the most part non-woody), but its constituent species show a remarkable degree of morphological variation (see Figures 35–43). From an evolutionary viewpoint, the genus is noteworthy because it is one of the few dicotyledonous herbs in which the vessel elements possess exclusively scalariform perforations (Takhtajan, 1954, p. 119). Furthermore, Meeuse (1966, p. 204) suggests that, "the pinnate or bipinnate leaves of the acaulescent Acrotremeae are also suggestive of a fern-frond, i.e., a pteridospermous-cycadopsid phyllome, and one of the possible habit forms of the 'reconstructed' group of Protodicots."

The genus has been generally considered to consist of about ten species and a number of varieties, all of which are confined to Ceylon with the exception of *A. costatum* Jack from Thailand and the Malay peninsula, and *A. arnottianum* Wight from southern India. Indications are that some of the species are very narrowly endemic and apparently quite rare.

The only comprehensive taxonomic treatments available are those prepared by G. H. K. Thwaites (1864) in his *Enumeratio plantarum Zeylaniae: An Enumeration of Ceylon Plants . . .*, by Hooker and Thomson (1872) for J. D. Hooker's *The Flora of British India*, in which they comment that *Acrotrema* is, "A remarkable genus of very variable species," and by H. Trimen (1893) for his *A Hand-Book to the Flora of Ceylon*. Trimen commented, "Most of the species are ill-defined and extremely variable, and I have failed to obtain any clear idea of their limits. They doubtless hybridise freely." Anatomical information is meager and accurate illustrations do not exist.

I recently had the good fortune to secure an excellent assemblage of well-preserved specimens of *Acrotrema* resulting from the collecting efforts of Dr. R. D. Hoogland of the Australian National University. The assistance Dr. Hoogland has given me now and in the past is acknowledged with much appreciation. Although many of these collections are currently without names, they are all vouchered and are being studied in

connection with a new generic treatment for a proposed flora of Ceylon.

The present paper draws attention to this uncommon and little-known dilleniaceous genus and provides additional morphological information, including the report of new anatomical features for the family.

MATERIALS AND METHODS

Liquid-preserved vegetative and floral material was received from Dr. R. D. Hoogland. Hoogland collection numbers *11423, 11460, 11469, 11572, 11575, 11580,* and *11583* were collected in Ceylon and have voucher specimens housed at the Commonwealth Scientific and Industrial Research Organization, Division of Plant Industry, Canberra, Australia (CANB); Department of Agriculture, Peradeniya, Ceylon (PDA); and the United States National Museum, Washington, D.C. (US). The Hoogland collection of *Acrotrema costatum* (*11635*) was obtained in Penang, Malaya, and has supporting material in CANB. Additional preserved plants of *A. costatum* were received through the efforts of Mr. K. C. Chiang at the Botanic Gardens, Penang. The following specimens of *Acrotrema* at the United States National Museum were also examined; these for the most part are very old sheets with Thwaites collecting numbers:

Acrotrema sp. **Ceylon:** *Thwaites* C.P. *3898*; *A. appendiculatum* Thw. **Ceylon:** *Thwaites* C.P. *3880*; *A. bullatum* Thw. **Ceylon:** *Thwaites* C.P. *239*; *A. costatum* Jack. **Thailand:** *Smitinand 2999*; *A. dissectum* Thw. **Ceylon:** *Thwaites* C.P. *3393*; *A. Gardneri* Thw. **Ceylon:** *Thwaites* C.P. *253*; *A. lanceolatum* Hook. **Ceylon:** *Thwaites* C.P. *2660*; *A. rugatum* Thw. **Ceylon:** *Thwaites* C.P. *3899*; *A. Thwaitesii* Hook. **Ceylon:** *Thwaites* C.P. *3364*; *Thwaites* C.P. *3969*; *A. uniflorum* Hook. **Ceylon:** *Thwaites* C.P. *3486*; *A. Walkeri* Wight. **Ceylon:** *Thwaites* C.P. *694.* Material of *A. arnottianum* was not available for study.

Histological details were revealed primarily through the use of paraffin-embedded and sectioned material subsequently stained with safranin-fast green or lacmoid. Several flowers and leaves were also cleared with 5% NaOH to study vasculation. Epidermal features were examined by making peels from preserved leaves. Pollen was acetylized and mounted in glycerine jelly.

The assistance of Miss Marion Seiler, staff artist in the Department of Botany, The University of North Carolina, Chapel Hill, is sincerely appreciated.

GENERAL MORPHOLOGY

The genus *Acrotrema* is composed of perennial herbs with simple leaves. Surprisingly, Hoogland (personal communication) mentions collecting specimens which were epiphytic. FIGURES 35–43 illustrate some of the variability in lamina dissection. FIGURES 35, 36, 37, and 38 represent plants with leaves that are undivided and generally obovate-oblong. The

leaves of *Acrotrema gardneri* (FIGURE 39) are narrowly oblong to linear-spathulate whereas those of *A. lanceolatum* (FIGURE 40) are characteristically linear-lanceolate in outline. The margins are entire, serrate, or dentate. FIGURES 41 and 42 show specimens of *A. Thwaitesii* with linear-lanceolate, pinnatifid leaves. The most dissected situation occurs in *A. dissectum* (FIGURE 43) in which the leaves are bipinnate with the largest segments deeply cleft and one or more pairs of small segments situated between the large ones. *Acrotrema lyratum* (not pictured) is described as having lyrately lobed leaves with four to five pairs of basal lobes, and *A. arnottianum* has been pictured as possessing large, entire leaves (Swamy & Periasamy, 1955). A study of the stability of leaf morphology in this genus in addition to chromosome data would be of interest. Thwaites's collection of *A. appendiculatum* Thw. (C.P. *3880*) is distinguished by the presence of rows of large, circular cushions between the secondary veins of the leaf (FIGURE 37). The foliage of *A. costatum* and many of the Ceylonese plants is variegated along the midrib as shown in FIGURE 20. The petioles sheath the stem and possess membranous, caducous wings. Young leaves exhibit conduplicate vernation (FIGURE 29) as is characteristic of other Dilleniaceae.

The stem is typically very short and in some cases the plants appear acaulescent. *Acrotrema costatum* (FIGURE 20) has a comparatively elongated axis which is readily divided into a pubescent aërial segment bearing crowded leaves and leaf scars, and an underground rhizomatous portion. With the exception of the primary root, all roots are adventitious. The endogenous origin of the roots from the stem has been illustrated in *Plate I, Figure 4* of Dickison (1969).

The inflorescence is a terminal or axillary raceme, occasionally reduced to a single flower. Each flower is subtended by a membranous bract. The length of the peduncle and degree of pubescence has been used to separate species. On the basis of general floral morphology, *A. costatum* from Malaya (FIGURES 9–15) is clearly distinguishable from most species inhabiting Ceylon (FIGURES 1–8). In the latter, the androecium is externally fasciculate with three stamen fascicles alternating with three carpels (*A. Thwaitesii* is an exception). Individual stamens possess long filaments and short anthers which open by longitudinal slits (FIGURES 6, 8). The androecium of *A. costatum* does not show external fasciculation but rather the fifteen stamens arise from the receptacle uniformly around the carpels. Stamens have elongated microsporangia which dehisce by apical pores (FIGURE 12). The gynoecium is usually described as consisting of three basally connate carpels; however, I have examined racemes in which some or all of the flowers were bicarpellate (FIGURE 11). The morphology of the carpels agrees essentially with previous descriptions (Dickison, 1968). Carpels are glabrous and differentiated into a swollen ovary and slender, sometimes recurved, style terminated by an indistinct stigmatic surface. The two or three conduplicate carpels are laterally concrescent (FIGURES 25, 26). At the level of placentation the ventral suture opens to produce a central cavity. Progressing distally, the

carpels close and become totally apocarpous at the initiation of the stylar region. The bicarpellate gynoecium of *A. costatum* has an opposite orientation as interpreted by Wilson (1965). The ovules are arranged in two rows along the placenta and range in number from two to many. Raphides are a characteristic feature in the carpel wall. The fruit is a follicle and the seeds are arillate. The flowers have five pubescent sepals and five glabrous petals which contain numerous raphides.

VEGETATIVE ANATOMY

Trichomes. The trichome complement of *Acrotrema* is unusually diverse and includes types previously unknown for the family. A dense pubescence may cover the aërial stem (FIGURE 20) and also young floral buds, pedicels and peduncles (FIGURES 1, 9, 10). On the leaf, hairs are conspicuously abundant along the major veins of the abaxial surface and margins of the lamina. Foliar trichomes are not uniform in length but are noticeably longer along the veins than in intercostal regions.

Compared to other Dilleniaceae, the prevalent trichome type is a unicellular, unbranched form. Frequently, however, these hairs are raised on pedestals of enlarged cushion cells (FIGURE 24), a feature not typical among other members of the family. A few septate hairs with varying numbers of cells and their outer walls divided into two layers were observed (FIGURE 23).

Acrotrema also possesses glandular trichomes. Glandular hairs are very abundant on sepals and to a lesser degree on the leaves. One type of glandular hair consists of a multicellular stalk and globose head (FIGURE 18), the contents of which stain very darkly. Another form observed on the leaves of *A. costatum* is composed of a cluster of swollen cells situated in depressions on the lower surface of the lamina (FIGURE 34). A third category of glandular trichome, which is very abundant on sepals and pedicels of *A. costatum*, is the most complex and diagnostic in the entire family. As seen in FIGURES 16 and 17, these trichomes are basically two-armed with a short stalk and spreading, multicellular arms that terminate with a much enlarged, clavate, thin-walled cell. This trichome is exceptional for the family and has surprisingly been overlooked in previous descriptions of the genus.

Leaf. Dorsiventral. Hairs of the type described above. Epidermis is composed of uniformly thickened, thin-walled cells. Cells of the abaxial epidermis tend to be isodiametric with straight walls whereas those of the adaxial surface are noticeably more sinuous. Costal cells are elongated and trichomes are surrounded by specialized "accessory cells." Stomata are abundant and confined to the abaxial surface (FIGURE 31). Mature stomata are anisocytic (*sensu* Metcalfe and Chalk, 1950), i.e., three subsidiary cells of which one is smaller than the other two, surround the stoma (FIGURE 33). This is the first report of the anisocytic stomatal pattern in the Dilleniaceae. Guard cells have an average length of 26 μ

FIGURES 1–15. Floral morphology of *Acrotrema*. 1–8, *Acrotrema* sp. (from *Hoogland 11469*, Ceylon). 1, Lateral view of open flower, × 2; 2, open flower seen obliquely from above, × 3; 3, flower seen obliquely from beneath, × 2; 4, gynoecium of 3 carpels, × 3.5; 5, petal, × 3; 6, stamen, × 6; 7, sepal, × 3; 8, anther, showing longitudinal dehiscence, × 6. 9–15, *A. costatum* (from *Hoogland 11635*). 9, Oblique view of flower from above, × 2; 10, same, from beneath, × 2; 11, lateral view of bicarpellate gynoecium, × 3.5; 12, front view of stamen, × 4; 13, same, from side, × 4; 14, sepal, × 3; 15, petal, × 3.

and contain numerous chloroplasts. The mesophyll is differentiated into palisade and spongy layers although they are not sharply defined (FIGURE 31). A weakly differentiated hypodermis is evident in *A. costatum*. Raphides are common. Subepidermal layers of collenchyma occur around the midrib. I have drawn attention elsewhere (Dickison, 1969) to the marked differences in petiole vasculation between *A. costatum* and the

Ceylonese species, where initially three bundles give rise to an abaxial arc of vascular tissue and an adaxial bundle. The petiole of *A. costatum* is supplied by a large number of traces (ca. 9) which divide in the mid-rib to become orientated as thirteen widely separated collateral bundles (FIGURE 19). The larger bundles have outer sclerenchymatous caps. A large central bundle is located adaxially, above which a conspicuously smaller bundle occurs with inverted vascular tissue. In species with un-dissected leaves, the vasculation of the lamina is pinnate with strong secondary veins terminating at the margins (FIGURE 20). Many species from Ceylon have secondary veins which fork noticeably at the margins (FIGURE 22), not a common feature among other dilleniaceous genera.
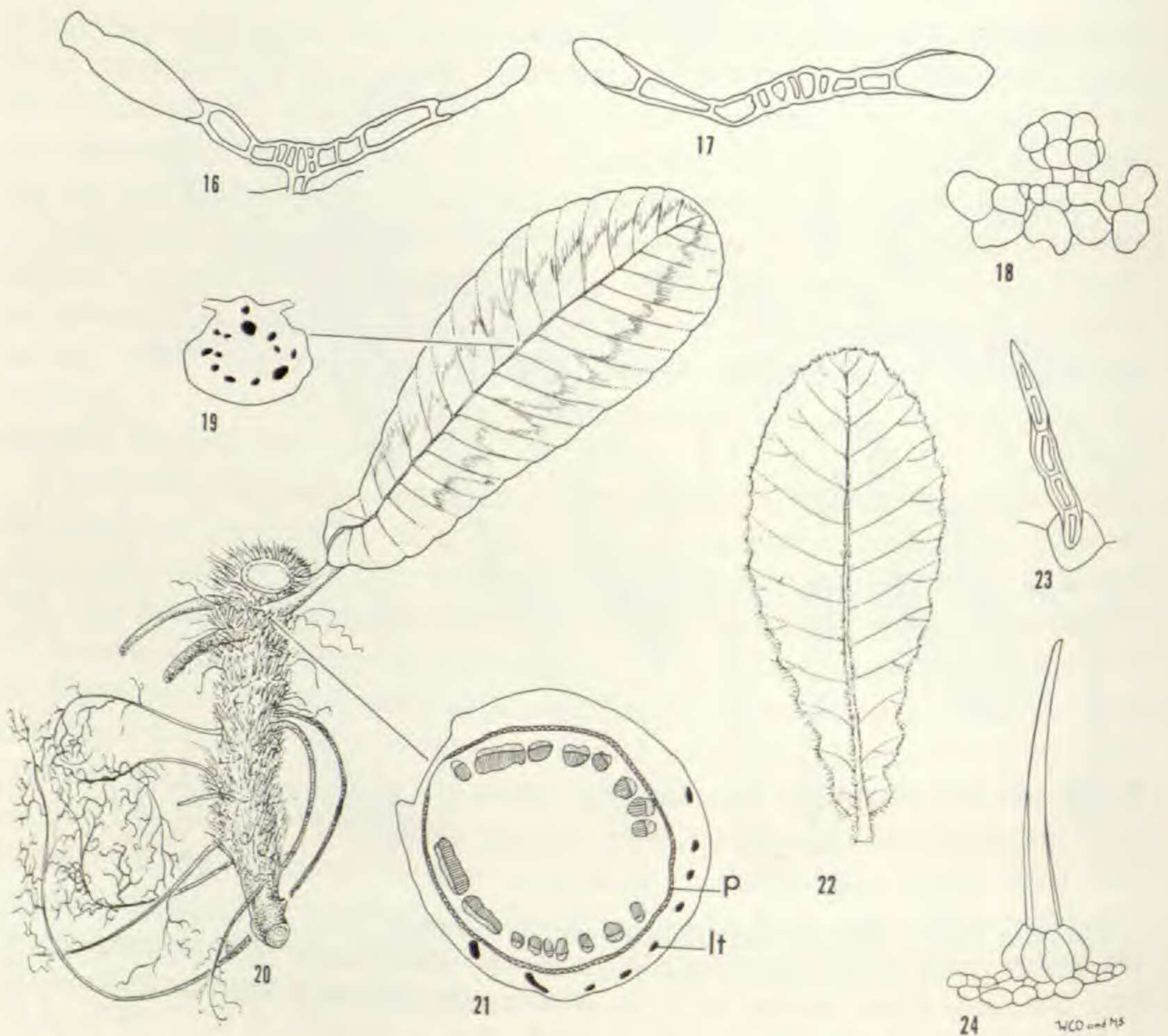
FIGURES 16–24. Vegetative morphology of *Acrotrema*. 16, Lateral view of glandular trichome from sepal of *A. costatum* (*Hoogland 11635*), × 62; 17, same, seen from above, × 62; 18, glandular trichome from sepal of *Acrotrema* sp. (*Hoogland 11423*), × 62; 19, transverse section through midrib of leaf of *A. costatum* (from Penang, Malaya, *s.n.*) showing widely separated vascular bundles, × 4; 20, habit of *A. costatum* (from same coll.), × 1/2; 21, transverse section through stem at nodal level showing departing leaf traces (lt), initia-tion of periderm (p), and eustele composed of collateral bundles, × 4; 22, leaf of *A. walkeri* (*Thwaites* C.P. *694*), showing pubescence and pinnate venation, × 1/2; 23, multicellular, unbranched trichome from the sepal of *Acrotrema* sp. (*Hoogland 11423*), × 62; 24, unicellular trichome elevated on pedestal, from sepal of *A. costatum* (*Hoogland 11635*), × 62.